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**Critical Literature Review
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A review of genetic differentiation of a population of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica.

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A review of genetic differentiation of a population of Weddell seals

(*Leptonychotes weddellii*) in McMurdo Sound, Antarctica.

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Weddell seal (*Leptonychotes weddellii*) hauled out onto sea ice in McMurdo Sound.

Image source: <http://www.discoverwildlife.com>

Abstract

The circumpolar distributed Antarctic Weddell seal (*Leptonychotes weddellii*) is considered sensitive to climate change, due to its disappearing fast ice breeding habitat, and assumed to have little panmixia due to a high degree of natal site fidelity. The advancement of molecular techniques has greatly assisted the understanding of population structure within this still cryptic species, and is beginning to reveal a significant relationship between the retreating ice edge extent and decreasing seal population size. However, there is still a need to investigate population trends at a continent-wide scale, to fully understand the climatic changes occurring in relation to the charismatic megafauna.

Introduction

Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica have been continuously studied for nearly fifty years (Smith 1965); despite this, their population biology is still not well understood. As fast ice-obligate breeders, the females tend to remain sedentary within their natal site, with a breeding regime structured around cracks in fast ice; males will defend a harem quite vigorously, leading to a level of polygyny greater than most other aquatically breeding seals (Gelatt 2001). This exhibited site fidelity was the basis for the hypothesis for decreased gene flow between populations (Davis *et al* 2008). However, while the adult males and females breed and pup at established fast ice sites, juveniles will “see the world”, so to speak, sometimes travelling hundreds of kilometres away from where they were born (Burns *et al* 1999). Others will vanish underneath the fast ice, passing many breeding colonies on their journeys around the coastline, while in one season at least one pup ended up over 700km away (Burns *et al* 1999); although recruitment into other colonies cannot be confirmed, there is the potential for gradual gene flow amongst populations. Unfortunately for Weddell seals, fast ice is rapidly disappearing within the Antarctic; unequivocal evidence for increases in global average air and water temperatures – leading to widespread melting of snow and ice – has been confirmed (IPCC 2007). This removes the primary breeding habitat, and it is not known exactly how critical fast ice is to the breeding ecology of this species. Breeding females experience a decrease in their foraging success and pup incidence directly related to ice floe structure and size (Siniff *et al* 2008); potentially, if the warming trends continue, genetic bottlenecks may occur as a practically nil percentage of pups emigrate to other populations. It needs to be understood how much

ice extent can be lost before this predicted decline is seen in genetic differentiation between seal populations, and bottlenecks begin to occur (Forcada *et al* 2012).

This paper aims to summarise the extent of isolation of Weddell seal populations within the Antarctic continent, and the effect a warming oceanic environment will have on the level of segregation of this species.

Review and Discussion

Despite extensive study of the McMurdo Sound populations of breeding Weddell seals (*Leptonychotes weddellii*), relatively little has been done with regards to genetic studies to determine the extent of segregation at a base molecular level. This may be due to the comparatively recent technology of non-invasive genetics, but it is most likely attributable to the inaccessibility of the study populations, in their fast-ice habitat.

Croxall *et al* 1992 described the seals as an unexploited, stable species, which exhibited a four to six year fluctuation in reproductive rate in phase with the Southern Oscillation Index, despite a shift in cycle periodicity. This is the beginning of a wealth of modern studies into the population structure of this species, continued over the next two decades with progressively advancing technology.

Emigration rates into and out of the area are vital in knowing how isolated the McMurdo Sound populations are, as this will assist in describing the amount of gene flow around the continent. As it stands, fewer than 25% of pups born in the Erebus Bay breeding aggregation are recruited back into this population; however there are low sighting probabilities for individuals less than six years old, and it is not known if they have been recruited into other colonies, killed, or just haven't yet returned to their natal site (Burns *et al* 1999). While recruitment into other breeding colonies by these individuals cannot be established, the long distances travelled by some pups (at least one pup ended up over 700km away) do indicate the potential for gradual gene flow amongst populations within the Ross Sea region. Given the vast array of knowledge available regarding Weddell seal behaviour and physiology during the summer months, this absence of pup data (especially for the period of their first, critical winter) is particularly conspicuous.

Weddell seals exhibit a unique mating system within the Antarctic; it is entirely structured around cracks in land-fast, where females will haul out to give birth and nurse their pups, and this results in a level of polygyny higher than that of other seals which breed aquatically

(Gelatt 2001). This is important to gene flow, as even though this species displays site fidelity during pupping season, some females have bred at colonies other than where they gave birth. With regards to the males, some may almost never haul out during the breeding season, as they are actively defending their harems; experience preserving mating rights gained over time is necessary for successful competition within breeding populations (Gelatt 2001).

Davis 2004 mentions that while polygyny is most definitely present in Weddell seals, it is not to the degree seen in land-breeding pinnipeds. While land-fast ice is a potentially unlimited surface for birthing, females will only use areas where predictable breathing holes form from ocean currents, weak spots, or polynyas; this confines the number of holes females are able to access, so many utilise the same holes to access the water. Males, as mentioned before, defend these holes for mating rights. However, ice is inherently variable; the interannual differences like glacial movements and tides, as well as innate female sociableness, help to create small levels of panmixia in populations. Because of all the above, Davis 2004 discovered Weddell seal breeding colonies are moderately structured across geographic scales; however, at this stage, due to the limited number of studies determining pinniped population genetics, major patterns could not be determined.

Building on the work conducted by Burns *et al* 1999, Cameron and Siniff 2004 reported a minimum 15% emigration rate *out of* McMurdo Sound; this correlates the hypothesis of low amounts of gene flow occurring around the entire Antarctic continent, i.e. that breeding populations are not entirely segregated.

This study also found that emigration rates are quite difficult to detect by experimental methods, due to the difficulty and expense of monitoring all the source populations in such a remote location, but immigration of individuals into McMurdo Sound was needed in some years to account for the size of the observed population. For example, in the 1997 season, reduced sea ice extent in McMurdo Sound was positively correlated with a large number of seals within Erebus Bay. This suggests seals abandoned preferred breeding areas due to the lack of fast ice, and seals that usually overwintered further north were granted easier access to Erebus Bay. But by 1998, the sea ice had extended further north, and the number of breeding individuals within Erebus Bay had declined, suggesting many of the previous year's immigrants had not returned. This was the beginning of correlating ice edge extent

with Weddell seal population size, and for both males and females it was a significantly negative association.

Davis *et al* 2008 presented four factors that influence population structure in Antarctic pinnipeds; in decreasing order of importance, natal homing, geographically variable vocal ranges, female sociability, and the ability of dominant males to limit or reduce access to reproductive females. The Weddell seal is the only Antarctic pinniped known to exhibit all of these characteristics.

The movement of adult seals throughout the winter season (from autumn freezing through to ice breakup in the spring) is restricted; although some seals may be found in summer offshore pack ice, especially pups and non-breeders, adults will generally overwinter in natal colonies or in a nearby area and return to breeding sites in early spring for reproduction.

Davis *et al* 2008 conducted some significant genetic work, especially in relation to the population structure of Weddell seals. Population structure was discovered at a minimum geographical distance of approximately 700km, while no significant population structure was uncovered at smaller scales. This suggests dispersal over relatively short distances (less than 700 km) results in enough gene flow to effectively homogenise populations at this scale, i.e. populations less than 700 km apart would be genetically indistinguishable from one another. This genetic distance between breeding colonies was significantly correlated to geographic distance, supporting the hypothesis of dispersal range being the major limitation to recruitment of an individual to a breeding colony that is not their natal site. Juveniles are the most likely method of gene flow between populations.

Davis *et al* 2008 also discovered a north-south dimension to Weddell seal segregation. Islands to the north have a high degree of differentiation; however this was not unanticipated, as it suggests long distance movements are rare. The isolation of these populations was expected due to the large distances required to travel to them, as well as the great expanses of unsuitable seal habitat which exist between them and coastal breeding colonies. However, it is not just northern populations which are inaccessible to the majority of the continental breeding individuals; Weddell seals can become physically isolated to the south of their range as well. White Island, within McMurdo Sound, hosts a small, apparently isolated breeding colony, separated from nearby McMurdo Sound populations by 20 km of ice shelf. No exchange of tagged individuals has ever been recorded between White Island

and populations in south-eastern McMurdo Sound, which suggests the colony is completely cut off. Genetic studies conducted by Gelatt 2001 determined the founding of the colony was within the last 100 years by less than ten individuals, and the results of Davis *et al* 2008 indicate low levels of genetic variation than other populations of Weddell seals, and distinct genetic differentiation. This colony also presents high mortality of pups and a reduced reproductive rate, which may indicate inbreeding depression and a potential genetic bottleneck.

With regards to the relationship Weddell seals have with their preferred fast-ice habitat, Siniff *et al* 2008 discovered that females were more likely to birth their first pup during a spring following a winter with more sea ice in the Ross Sea region, i.e. a winter often following a summer of minimal ice. An insight into the demographic consequences of long-term oscillations in fast-ice perseverance was presented in 2000 when a large portion of the Ross Ice Shelf broke off into Iceberg B-15; this iceberg subsequently blocked the usual movement of sea ice from McMurdo Sound until winter 2006. As a direct result of this event, fast ice increased in thickness, extent, and seasonal persistence. Weddell seals were directly affected from this event, as the ice increased in thickness, making it harder to maintain breathing holes, as well as cracks closing which had been predictably present in previous years. As a result of this, less adults were present for breeding, and a smaller number of pups were born; however, it is unknown if the usual McMurdo Sound females pupped at other locations. This iceberg event prompted Siniff *et al* 2008 to discover that over a ten year period, a strong negative relationship existed between ice thickness and the number of pups born in McMurdo Sound, i.e. the thicker the ice was, the less pups were birthed. However, once the iceberg had removed itself from the Ross Sea region, and the ice levels had begun to return to normal, the number of pups born returned to previous levels remarkably quickly.

The level of fast ice in Weddell seal habitat is critical. Too much and females can't access preferred breeding sites, as evidenced by the Iceberg B-15 event, but too little and they do not have a safe substrate on which to pup. For example, weekly counts of seals from 1974 from various shore locations in Arthur Harbour, in the Antarctic Peninsula region (in the vicinity of Palmer Station), show that Weddell seal population numbers have gradually declined. The cause of the decline is as yet unknown, but it is strongly assumed to be

connected with the reduction in suitable fast ice breeding habitat, especially since the Antarctic Peninsula is one of the fastest warming oceanic areas on the planet (IPCC 2007). Curtis 2009 conducted extensive genetic work on multiple species of Antarctic seals, and if the White Island population is disregarded, there is no evidence for a recent, sustained genetic bottleneck in Weddell seals. This could be interpreted as the reduction in sea ice is not adversely affecting this species; however, it is more likely that the populations have simply not had time to develop bottlenecks yet, as the fast ice is disappearing too rapidly. Costa *et al* 2010 echoed this, with the diving behaviour of Weddell seals restricting them to inshore, intermediate depths, and thus having to remain quite resident in areas where the decrease in fast ice will most likely impact their available breeding and foraging habitat. Forcada *et al* 2012 continues the trend of attempting to correlate fast ice loss with declines in Weddell seal numbers. While their study exhibits significant declines in suitable habitat for this species in FAO Area 48.1, they also raise the point that to date, there has only been one long-term study at Anvers Island in the Antarctic Peninsula which indicates a confirmable decline for a single Weddell seal colony. This emphasises a need to investigate population trends for a species at a much wider scale to fully comprehend the changes occurring in the Antarctic. This study also identifies that it isn't clear exactly how critical fast ice is to this species – especially since it is not known of other areas they may use to breed in the absence of ice – and it needs to be understood how much ice loss can occur before seal populations are likely to decline.

Rotella *et al* 2012 brings together population genetics and environmental variables to comprehensively describe the situation in which Weddell seals find themselves. For this large, long-lived species, environmental variation should have the least effect on the survival of the adult population, but will impact much greater on the survival and reproductive capabilities of younger cohorts. For example, this particular seal species is unable to buffer from a lower average survival rate when they birth a pup, most likely due to their heavy dependence on a capital breeding strategy (where extreme reductions in body mass occur when they rear a pup); if the survival rate for a breeding female is already lowered by environmental conditions from when she herself was born, the species will undoubtedly suffer as gene flow within populations (and as a flow-on effect, between populations too) is markedly decreased.

This study also explains that broad-scale environmental conditions in the Ross Sea, rather than fine-scale ones at colony level, are the important drivers for Weddell seal population dynamics. This is supported by females exhibiting similar patterns of vital rates, in spite of the fact that females of different ages and breeding states appear to reside in different locations, at least during the breeding season.

Conclusions

Weddell seals have been studied continuously in McMurdo Sound for over fifty years, and they are the best-studied of the Antarctic pinnipeds. However, identifying the extent to which a species is isolated in one of the most isolated environments on the planet will always pose some challenges. The advancement of molecular techniques has greatly assisted the understanding of population structure within this still cryptic species, and provided some insight into how they will be affected by rapidly occurring climate change. Long term datasets are invaluable in this regard, as they provide snapshots through time, and despite constantly changing scientific techniques, trends can still be drawn from them; for example, the correlation between declining sea ice and declining Weddell seal numbers at Anvers Island on the Antarctic Peninsula (Forcada *et al* 2012).

Future research needs to take into account just how rapidly the climate is changing when studying population dynamics of Weddell seals, and how they will be affected by the changing climate; for example non-ice breeding populations may have completely different natal site fidelity or polygyny levels than ‘traditional’ colonies. Immigration and emigration rates may vary as ice become less abundant, and thus populations may be compressed into regions that cannot sustain high levels of this species; conversely, colonies may be isolated even further. As yet, there is no evidence for a genetic bottleneck within the circumpolar distribution of the Weddell seal (Curtis 2009); however, if the observed trends in population isolation on relatively small dispersal scales continue, combined with massive fast ice reduction, this species may very well be under the very real threat of dramatic gene loss within the species.

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